Evolution of Self-Organized Systems

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Abstract. In this paper I ask questions about the evolution of self-organized activity cycles that are found in some ant colonies. I use a computer model that generates periodic activity patterns in interacting subunits and explore the parameters of this model using a genetic algorithm in which selecting on one aspect of the system produces the distinctive self-organized pattern. The general point that I explore, using the example of activity cycles, is that the observation of a self-organized pattern does not mean that the pattern is an adaptation. Self-organized patterns can represent non-adaptive correlated responses to selection, exaptations or even selectively disadvantageous traits. Evolution of self-organized patterns requires genetic feedback between the self-organized output and the subunits that produce the pattern. Without this necessary feedback, a self-organized system does not evolve.

Introduction

Many features of biological complexity result from self-organization. Biological systems are, in general, global patterns produced by local interactions. The biological structures that seem closest to the ideal of directed organization are proteins that arise from a coding sequence of DNA. Even here, the complex folded structure of a protein is not simply coded in the DNA sequence. Protein structure is the result of genetic and epigenetic processes that produce a single or a few appropriate folded structures from the huge number of stable and thermodynamically equivalent structures. Their structure is not specified uniquely by some central pattern generator, the DNA sequence, but requires

interactions among all of the molecular machinery of the cell, including DNA, RNA, and other proteins (Voet and Voet, 1995).

The adult body plan of an organism is a self-organized system produced by the complex interactions among cells and tissues mediated by differential gene expression, local chemical communication among cells, and local regulation that constitute development. The development of an organism is not simply coded by the DNA sequence, but is again a process that is produced by a complex, self-organized system with genetic and epigenetic components (Goodwin 1994; Solé and Goodwin, 2000).

Because social insect colonies are intermediate in their degree of integration between a single soma and a collection of unconnected individuals, they have been favorite subjects for studies of self-organization (see, *e.g.*, Camazine *et al.*, 2001). This same intermediate position in the levels of genetic integration also makes social insects favorite subjects for studies on levels of selection, cooperation, and conflict. The purpose of this paper is to look at an example of selection operating on colony functions to change interactions among workers in such a way as to alter the self-organized activity patterns of the colony.

One of the appealing aspects of the study of self-organized systems is that we do not need anything specific from biology to understand the existence of self-organization. Self-organization occurs for reasons that have to do with the organization of the interacting elements. When we recognize that the same ripple patterns that can exist in sand dunes also exist in biological patterns, some of us feel a profound sense of connection between the physical processes and the biological ones. However, it is undeniable that biological self-organized systems have a capacity that nonbiological self-organized systems usually do not have. Inheritance produces temporal continuity that causes a sort of memory in the system. The difference between the essentially nonbiological self-organized systems and the self-organized systems that most biologists are interested in is

that sand grains have no system of inheritance. The sand grains do not produce more sand grains that behave in similar ways, or more importantly, with slight modifications. The pattern of ripples in the sand can be changed only by changing the external conditions or by making a qualitative change to the material of which the sand is composed. In biological systems, inheritance allows individual "sand grains" to persist with slightly altered rules for interaction.

Biological self-organized systems should be interesting to those who study self-organization because the inheritance that is intrinsic to biological systems gives them a level of complexity that is unique. Biological self-organized systems should be of interest to evolutionary biologists for two reasons. The first is that self-organized systems produce phenotypes that are subject to selection or other evolutionary processes. Secondly, evolutionary processes may operate on the inherited elements of self-organized systems. These elements may be the subunits (e.g., cells or organisms), but more interestingly, they may be the interactions among subunits. Systematic, microscopic changes in interactions can produce sudden macroscopic phase-shifts in the behavior of self-organized systems, and thus in the phenotype of a organism. This is a characteristic of complex systems in general (e.g., Bak et al., 1988; Kauffman, 1993; Goodwin, 1994; Solé and Goodwin, 2000), but natural selection is a mechanism that produces these systematic microscopic changes. A corollary is that selection on one aspect of a biological self-organized system can produce dramatic changes in some other aspect of the phenotype. This duality between levels of organization of the output of a self-organized system and the interacting components mirrors the duality in levels of selection, or indeed between phenotype and genotype. A standard caveat from evolutionary biology that I develop in this paper is that we must be careful when we impute adaptation to the observation of self-organization, even a self-organized system that is subject to selection.

Evolution in a Self-Organized System

In this paper I examine the model consequences of selection operating on a complex interacting system. The consequence is the emergence of a self-organized property that is independent of selection operating on the system. The system that I describe is that of activity cycles in ant colonies. I use models of ant activity in which colonies can vary in size and in how the worker ants interact with one another. Using a genetic algorithm, I allow the population to evolve in colony size and in the types of interactions. Fitness is assigned to colonies on the basis of a trait that is independent of the degree of periodicity in the colonies, that is, independent of the expression of the self-organized phenotype.

The point that I want to make in this section is that

selection on a complex system can result in self-organized patterns even when these patterns have no selective consequence themselves. When we observe self-organized systems, we are under no compulsion to assume that the pattern represents an adaptation. The general point that changes, even when produced by selection, do not represent adaptations has been made for such diverse examples as the variety of patterns of the sutures of ammonite shells (Gould, 1977) and the changes in allele frequency due to genetic hitchhiking (Hedrick, 1982). Specifically, I examine an instance of a self-organized trait that occurs as a correlated response to selection.

The metaphor that I use to make these points is ant colony activity cycles. The activity within colonies of certain species of ants is characterized by short-term cycles (Franks et al., 1990; Hemerik et al., 1990; Cole, 1991a, c, 1992; Tofts et al., 1992; Cole and Cheshire, 1995; Cole and Trampus, 1999; Boi et al., 1999). These activity patterns, while by no means perfectly periodic, have a substantial periodic component. The periodicity is not a property of individual worker ants since they have activity patterns that are either random or chaotic (Cole, 1991b, 1994). As larger numbers of worker ants are added to an experimental aggregate, the magnitude of the largest periodic component increases (Fig. 1a; Cole and Cheshire, 1995). The periodic activity of colonies represents a self-organized temporal pattern. There is a spatial component to this pattern as well, since activity spreads in a traveling wave throughout the colony (Cole and Trampus, 1999; Boi et al., 1999).

Models of ant colony activity were first developed by Solé et al. (1992) and expanded and modified by Miramontes et al. (1993), Cole and Cheshire (1995), Solé and Miramontes (1995), Solé and Delgado (1996), Delgado and Solé (1997a, b, 2000). These models are mobile cellular automata (MCA) or fluid neural network (FNN) models in which an automaton (a worker ant) becomes active spontaneously and, when active, may move through the gridded nest. The level of activity declines spontaneously at a constant rate, until a threshold level is reached. Neighboring ants may also influence each other's activity depending on the types of interactions that are allowed—that is, depending on the rule set for interactions. For example, we may allow an active ant to influence the activity of a neighboring active ant, or we may allow an inactive ant to influence the activity of a neighboring active ant. The influence of an active ant is to increase the activity of neighbors, and the influence of an inactive ant is to reduce the activity of neighbors. In this simplest model, we allow the ants to be in one of two states, active or inactive. Active ants have an activity level above a threshold, and inactive ants have an activity level below this threshold. The activity of each ant in subsequent time steps is computed according to an algorithm that describes how the activity of the ant changes through time on its own, and the effect of the interactions of
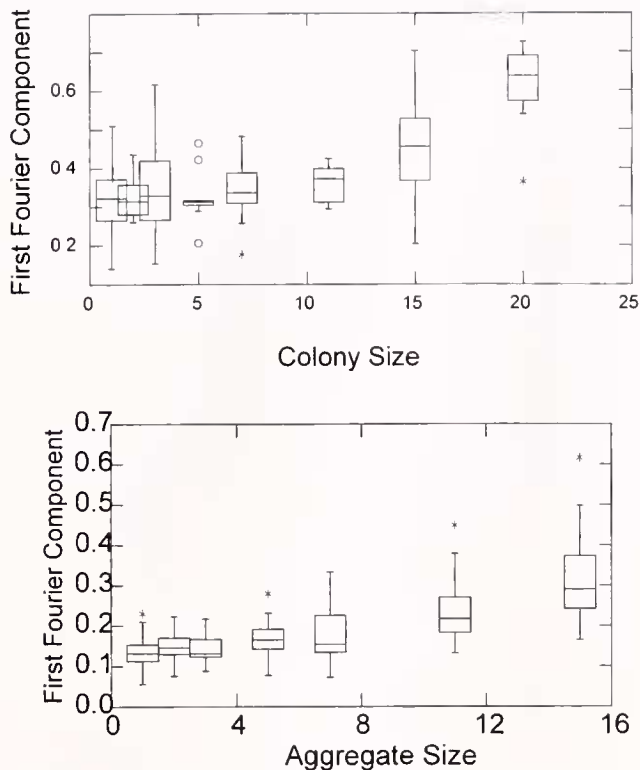
Figure 1. (A) Data from activity records of the ant *Leptothorax al-lardycei*. The number of individuals is given on the abscissa and the power in the first fourier component of the activity record is given on the ordinate. Activity records are at least four hours long. (B) Magnitude of the first fourier component in simulations of the MCA model described in the text for varying numbers of automata. These figures are adapted from data described by Cole and Cheshire (1995). (ˣCopyright 2002, The University of Chicago Press. All rights reserved. Used with permission.)

each of its neighbors. The details of the model can be found elsewhere (Solé *et al.*, 1992; Cole and Cheshire, 1995). The rule sets are coded by a matrix that dictates how active or inactive ants influence the activity of their active or inactive neighbors. Since we have two activity states for the ants, there are four terms in this matrix. The first term is the effect that an active ant has on another active ant. A value of 1 indicates that the interaction is allowed, and a value of 0 indicates that the interaction is forbidden. It is convenient to speak of $J_1 = 1$ rules, to indicate that active ants are allowed to influence the activity of other active ants. For example, $J_4 = 0$ rules would indicate that inactive ants are forbidden to influence the activity of inactive ants.

Since the four terms of the interaction matrix can be either 0 or 1, there are 16 rule sets that apply to this model. Earlier work (Cole and Cheshire, 1995) showed that if the model follows the rule $J_1 = 1$, then as larger numbers of workers are added to the system, the degree of periodicity of the simulated outcome increases in the same way that experimental results do (Fig. 1b). In other words, $J_1 = 1$ rule sets are necessary and sufficient to generate periodic activ-

ity; the other rules are not critical. Since we are speaking of social behavior, we might regard this as a social facilitation term.

Having $J_1 = 1$ means that active ants stimulate other active ants; in other words, there is a autocatalytic term. Since ants are allowed to move only one space step per time step, there is also an implicit time delay in the system as a whole. Active ants cannot influence ants more than one spatial step away. The activity pattern of the colony is due to a reaction-diffusion system (Murray, 1989) that exhibits self-organized activity cycles that occur as waves propagating throughout the colony.

However, the fact that these patterns can be produced does not mean that they represent an adaptation. The next step is to produce a model of the evolution of activity patterns and colony size in ants. I start with the assumption that activity cycles themselves have no functional or selective consequence. When I make this assumption in the model, I am not claiming that activity cycles have no functional consequence, I am just exploring the consequence of making that assumption. Delgado and Solé (2000) use the same models to consider possible increases in colony efficiency that may result from periodicity in activity. What I assume does have selective value is the rate with which an ant can traverse the colony. I take as a reasonable assumption that the longer the time that is required for an ant to move between specified locations in the nest (for example, from one side of the nest to the other), the longer the time required for food or information to travel through the nest. Provided food is carried by ants or information is propagated by physical contact, these are reasonable assumptions. The assumption that I am making is that colonies in which food or information or workers themselves travel more quickly from place to place have higher fitness. The fitness of a colony that has a particular rule set will be the reciprocal of the time required for transiting the nest.

The strategy is to take a model population of "ant colonies" and follow the changes in the rule sets used by colonies. Initially, all colonies are composed of three workers with $J_1 = J_2 = J_3 = J_4 = 0$; workers are not allowed to influence the activity of any other workers. In each time step, fitness is assigned by noting the transit time of workers within colonies that use particular interaction rules. Fitness varies with the size of the colony and the rule set that the colony is using. Fitness assignments were made by performing 10 simulations for each of the 16 rule sets using 3, 5, 7, 11, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, and 65 workers (since the same grid size is used, this results in increasing density). In each simulation a single transit time was measured. A fourth order polynomial was fitted to the relation of transit time and colony size to interpolate the nonlinear relationships. The polynomial was then used to calculate transit time, or 1/fitness for a particular combination of rule
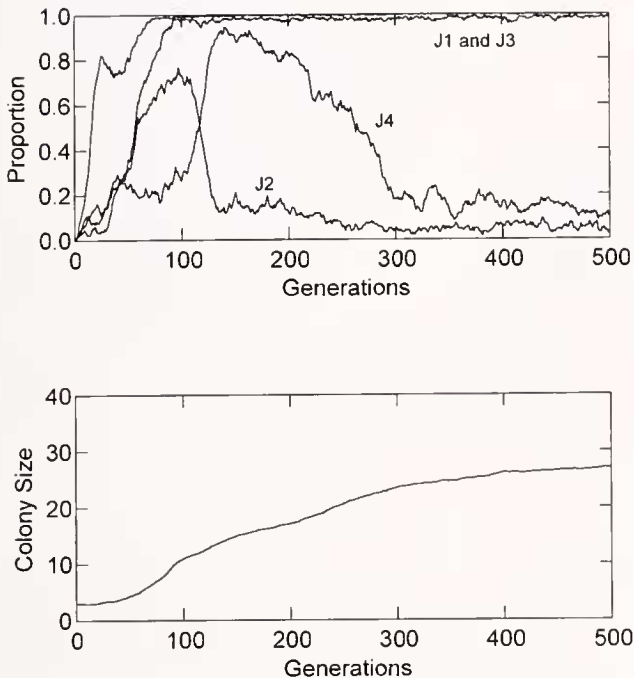
Figure 2. The outcome of selection for various rule sets in the genetic algorithm described in the text. (A) The proportion of colonies that obey the $J1 = 1$, $J2 = 1$, $J3 = 1$ or $J4 = 1$ rule through time, starting with a colony size of three workers with all workers obeying the rule $J1 = J2 = J3 = J4 = 0$. $J3 = 1$ becomes fixed in the population first, followed rapidly by $J1 = 1$. Both the $J2 = 1$ and the $J4 = 1$ rule transiently reach high proportions before declining in frequency. The $J1 = 1$ and $J3 = 1$ rules do not remain fixed due to recurrent mutation. (B) The average colony size of the 1000 colonies composing the population.

Entropy is, $\Sigma p_i \log_2 p_i$, summing over the proportion, p_i, of time that the aggregate spends in each of the $n + 1$ activity states (n = number of ants). If the ants behave independently, joint entropy equals the sum of the individual entropies and the mutual information is zero. If the ants remain in one behavioral state, then the sum of the entropies is low and the mutual information is low as well. For each aggregate I calculated the mutual information per pair of ants and analyzed their average values. The average mutual information per pair of ants is shown in Figure 3 for various rule sets. When selection operates on the speed of movement through the nest, the correlated effect is to increase the complexity of activity patterns. In this simulation, colony size and the rule sets coevolve to place the activity pattern near the peak of complexity, or in the region that Langton (1992) calls "edge of chaos."

Discussion

As with any complex trait, the observation of a self-organized pattern says little about the functional consequence of the pattern. In the model results, the self-organized structure is neither advantageous nor disadvantageous; it is simply nonadaptive. However, the self-organized trait could be disadvantageous if we measure the effect that increasing expression has on fitness, provided this effect is less than the increase in fitness gained through selection on the other trait. We might measure the effect that activity cycles have on fitness and detect a negative relationship. Provided the negative effects of activity cycles are more than balanced by the positive effects on transit time, particular rule sets that generate periodic activity could be at a selective advantage.

Finally, it is possible that a self-organized pattern could be produced as a correlated response but then be acted upon by selection in the future. Under a new set of circumstances, the self-organized pattern may have a positive effect. This would be an exaptation in the sense of Gould and Vrba (1982). Selection on the self-organized pattern may modify it to become more effective at producing these positive consequences; however, the self-organized pattern could not be regarded as an adaptation. Subsequent modifications to the system to produce additional changes should be regarded as secondary adaptations, although it would still be fair to regard the pattern itself as an exaptation. We could imagine, for example, that cycles of activity are produced in ant colonies by selection operating on the level of activity of individual worker ants. The existence of activity cycles may then be co-opted to improve certain colony functions according to the mechanism suggested by Delgado and Solé (2000).

Self-organized systems happen, but that may not mean anything. Logically, the possibilities are that they have no selective consequence (they are nonadaptive), they contrib-
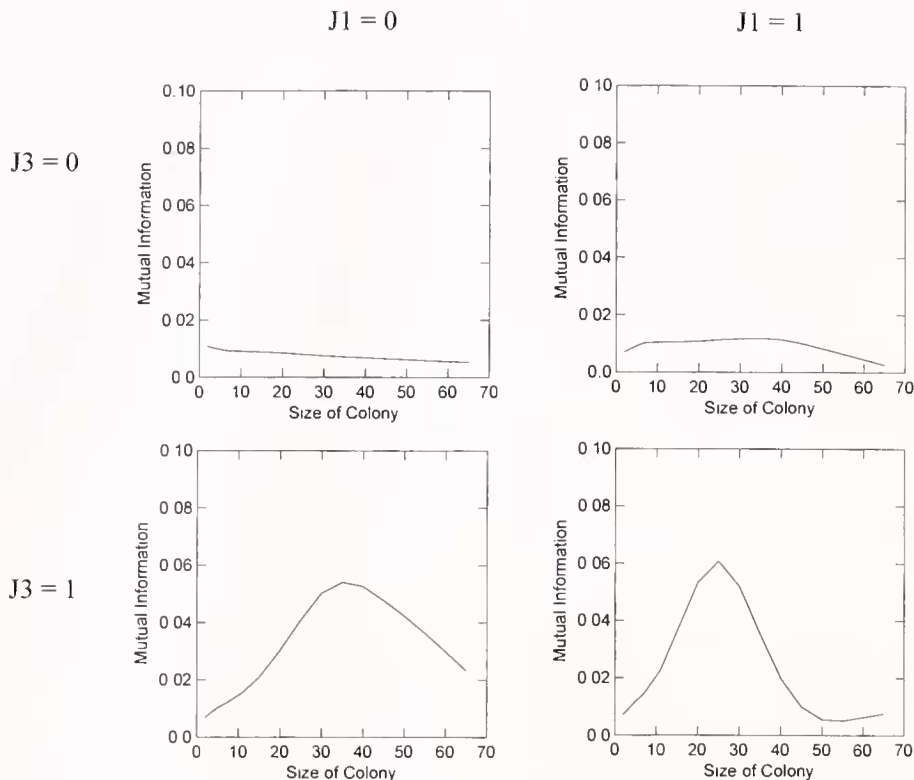
set and colony size. The mutation rate, going up or down in colony size (in one-worker increments) or changing one of the rules (from 0 to 1 or back) was 0.01. The population of 1000 colonies was repopulated by random replication of colonies with probabilities based on a colony's relative fitness.

The outcome of this genetic algorithm is shown in Figure 2a. Both rules $J_3 = 1$ and $J_1 = 1$ rapidly go to near fixation in the population. Other rules are transiently selected for because colony size is changing as well (Fig. 2b). Selection on transit time produced a rule set that generates self-organized activity cycles. These self-organized patterns are themselves not the outcome of selection; they have no effect on function or fitness, and yet they appear due to selection on transit time. They are a correlated response to selection.

A second consequence of this selection is that it produces activity patterns of greater complexity. For each rule set, I measured the complexity of the activity record as the average mutual information per pair of ants (Langton, 1992; Solé and Miramontes, 1995). The mutual information in a pair of activity records is the sum of the entropy in each ant's activity record minus the entropy in the joint activity record: entropy of ant 1 + entropy of ant 2 − joint entropy.

Figure 3.   The mutual information content of activity patterns for various rule sets and colony sizes. The different *J*1 rules are found across columns and the *J*3 rules are shown on the rows. These two rules are the only two that influence the degree of complexity of the activity patterns; other rule sets yield flat curves. The results are based on the average mutual information per pair of ants in 10 simulations for each of the colony sizes given in the text. The lines are a locally weighted scatterplot smooth (tension = 0.3).

ute to the fitness of an organism (are an adaptation), they contribute to the fitness of an organism as a consequence of a cooptation of the effect of self-organization (an exaptation), or they represent a trait at a selective disadvantage that is produced because of indirect selection.

The key distinction concerning the evolution of self-organized systems is whether they are anything different from ripples of sand on a sand dune. The key difference is inheritance. To the extent that the rules for a biological self-organized system can be inherited, they are more interesting than ripples of sand because they are subject to evolutionary change. This requirement places limits on the places where self-organization can evolve. If the fitness of the subunits in the interaction cannot be influenced by the self-organized pattern, then the pattern cannot evolve.

The self-organized pattern is produced by a feed-forward mechanism from the subunits to the pattern. In order for the self-organized system to evolve, there must also be feed-back between the self-organized pattern that emerges from the interaction and the units of action. There is clearly a genetic feedback between the elements that produce an organism (the cells, for example) and the self-organized phenotype of the organism. In most cases the subunits

composing the whole have near genetic identity. Hamilton (1964, 1970) and Price (1970) showed us how to think about the evolution of self-organized systems, such as social insect colonies, that do not have genetic identity, but genetic relatedness.

In the hierarchical organization of biological systems, there are limits to this progression. Take, for example, the self-organized wave fronts of migrating wildebeest herds (Gueron and Levin, 1993). These large herds characteristically form movement fronts with a wavelike structure that has a wavelength of kilometers, even though the local interactions among the wildebeest are occurring over the scale of meters. This is a self-organized structure where there is probably no genetic feedback between the emergent output and the actions of the subunits. It is unlikely that these self-organized patterns can evolve. Evolutionary processes operating at lower levels can change the rules of interaction that may lead to different forms of the wave front, but the form of the wave front is not evolving, in the sense that there are no evolutionary forces acting on the form of this wavefront. In a similar way, self-organized patterns of ecosystems that may emerge from interactions among the component species may not evolve either. If the

self-organized pattern itself has no influence on the reproduction of those that have inheritance, the self-organized pattern may change, but it does not evolve.

Acknowledgments

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